

Behavior of Infant Rhesus Monkeys and Their Mothers in a Free-ranging Band

JOHN H. KAUFMANN¹

Laboratory of Perinatal Physiology, National Institute of Neurological Diseases and Blindness, National Institutes of Health, Public Health Service, San Juan, Puerto Rico

(Plates I-IV)

INTRODUCTION

DESPITE the recent increase in primate field studies, there is relatively little known of the early development and socialization of infant monkeys in free-ranging populations. Such information is needed for an understanding of the behavior of primates in the field, and is highly desirable as a standard of comparison for the many studies of development and socialization that are conducted in the physically and socially restricted environments of laboratory colonies. For comparison with laboratory studies, information on rhesus monkeys (*Macaca mulatta*) is especially pertinent. Yet information on the behavior of rhesus infants in the field has been limited to brief observations by Southwick, Beg & Siddiqi (1965) in India, and by Altmann (1962) in the free-ranging colony on Cayo Santiago, a small islet off the east coast of Puerto Rico (see Altmann's report for a description and history of the colony).

Until recently, study of captive rhesus infants was confined to highly artificial situations in small indoor cages and "playrooms." Foley (1934), Hines (1942), Lashley & Watson (1913), Mowbray & Cadell (1962), and Tinklepaugh & Hartman (1932) all studied the individual behavior of infants. Hansen (1962) and Rosenblum (1961) included limited social interaction in their studies, and Harlow, Mason, and others (summarized by Mason, 1965) have made extensive studies of deprivation effects on socialization. Perhaps the most unnatural aspect of all these studies was the lack or great restriction of social interaction. Although such restric-

tion is necessary to obtain detailed, analytical results, it leaves the possibility that the behavior observed may be different, at least in its rate of development, from that of free-ranging monkeys in large groups. Certainly the socialization of laboratory monkeys fails to include frequent interactions with the many age and sex categories found in large bands.

In an effort to help bridge the gap between field and laboratory situations, Hinde, Rowell & Spencer-Booth (1964) studied the behavior of rhesus infants living in small social groups in outdoor runs. Their paper summarizes the results of previous laboratory studies, and presents abundant data that are directly comparable with data taken in the field.

In the course of other field work during the 1963 birth season on Cayo Santiago, I had an opportunity to observe the behavior of rhesus infants in a large, free-ranging band. This paper presents data on the behavioral development and social relations of infants up to three months old. Because the socialization of infant monkeys is inextricably bound to the social behavior of their mothers, the mothers' social relations during this period will also be considered.

METHODS

All of the data presented here were obtained from field observation of the colony's largest band during its 1963 birth season, which lasted from January 7 to May 4. During this period the band contained 40 mature females, 28 mature males, 35 immature females (1-3 years old) and 25 immature males. In this band 30 infants were born naturally on the island: 2 in January, 14 in February, 10 in March, 2 in April and 2 in May.

¹Present address: Zoology Department, University of Florida, Gainesville, Florida.

Four infants were delivered by cesarean section and taken from their mothers for use in medical experiments. I determined the social rank of the mature males and females by observing displacements at food and water, and the exchange of threatening and submissive signals. All of the monkeys but the infants were individually recognizable by physical characteristics and tattoos; the infants were identified by their association with their mothers.

I recorded as many as possible of the observed social interactions of infants and of their mothers, and paid particular attention to the first dates on which each infant performed significant new acts. Two females were selected for special study. One of these (11) was over ten years old with a long breeding history; the other (DR) was a four-year-old with her first infant. These two and their infants were watched for one to two hours each day, five to six days per week, during the first month after birth. Thereafter a special effort was made to observe them as often as practicable along with the other females and their infants. Approximately 70 hours were spent observing the other females and infants. Observations were made during all of the daylight hours, but were concentrated during the early morning when the monkeys were most active. Because every infant could not be observed continuously, I undoubtedly missed seeing many acts when they were first performed. My observations should, however, give a good idea of when each new act became common among infants of a certain age.

BEHAVIORAL DEVELOPMENT OF INFANTS

Table 1 summarizes the infants' behavioral development.

A newborn infant typically clung tightly to its mother's underside, alternately sleeping and nursing (Fig. 1). When she walked the infant remained clinging ventrally by its hands and feet (Fig. 2), though the mother might help support it at first with one hand. Infants clung unaided even when their mothers ran at top speed or joined in a fight. As early as the second day after birth some infants began sitting on the ground and standing shakily on all fours for a few seconds. At first they could hardly lift their heads and abdomens clear of the ground, but even so they sometimes crawled a faltering step or two before collapsing in a heap. Standing and walking improved rapidly and by the end of the first week advanced infants were able to walk several feet, though slowly and clumsily.

In the second week infants began actively exploring within three feet of their mothers, handling and mouthing plants, sticks and rocks. The

TABLE 1. BEHAVIORAL DEVELOPMENT OF INFANTS

Act	First day ever seen	Week when first performed by most infants
Stand on all fours	2	1
Crawl	2	1
Sit upright on ground	4	1
Stand upright (supported)	7	2
Stand upright (unsupported)	26	*
Handle and mouth plants, sticks, rocks	11	2
Hop (bipedal)	12	2-3
Jump (in trees)	41	7
Hang by legs and feet in trees	23	*
Climb		
On mother	7	1
On vines, bushes and trees		
Up to 1 ft.	11	2-3
Up to 3 ft.	16	4-5
10 ft. and above	47	7-8
Follow mother		
10 ft.	16	*
30 ft.	29	*
50 ft.	33	*
Ride on mother's back	4	1-6

*Not seen performed by most infants by end of study.

distances which infants traveled from their mothers were limited by the restraints imposed by their mothers more than by the infants' physical limitations, and these distances will be given in the section on infant-mother relations. A better indication of the infants' capabilities is the distance they walked in following their mothers when they were not carried. Thus one infant followed 10 feet on the 16th day and 30 feet on the 29th day, while two infants followed more than 50 feet at the end of the fifth week.

During the first week some mothers pushed their infants up onto their backs instead of carrying them below. This happened most often when the infant was sitting by the mother's side. At first the infant rode on her back for only a few seconds before falling to the ground; soon it clung precariously as she walked, frequently slipping low on her flank, shoulder or hip. By the end of the first week some infants rode on top frequently and adeptly (Fig. 3). In the time of first riding on their mothers' backs the infants were extremely variable. Though some became skilled during the first week, others did not begin until the seventh week, and approximately equal numbers began during each of the intervening weeks. The range was 4-45 days, the mean 22 days, the median 26 days, and there was no

clearly defined mode. Of all my observations of first dates for specific acts, these are probably the most accurate because infants riding dorsally are so conspicuous. One infant, extreme in this respect, began riding on its mother's back by the fourth day. During the next ten days it was seen riding 26 times, 10 of them (38%) on the mother's back. Even after they became proficient at riding dorsally, most if not all infants rode chiefly below for the first few months. Rarely I saw a female carrying her infant and a yearling at the same time, either with the infant below and the yearling on her back, or with the yearling below the infant and clinging to it.

The relationship between sex and rate of development was obscured by the crudity of the data, the relative permissiveness of the mothers and the preponderance of females among the early births (15-11 by April 1, though only 16-14 over-all). Females tended to ride on their mothers' backs sooner than males, but in most activities neither sex was clearly ahead.

SOCIAL RELATIONS OF INFANTS

The speed of an infant's socialization probably depends on the interplay of three factors: (a) the infant's own physical and mental char-

acteristics, (b) social facilitation, influenced by the infant's time of birth relative to its peers, and (c) the relative permissiveness of its mother. The effects of minor physical and mental differences between the infants could not be determined in the field, and no greatly accelerated development or gross deficiencies were seen. The possible role of social facilitation was not clear from this study, since all of the infants except female 11's had potential playmates from the start, and social play typically began when the infants were three to four weeks old. Female 11's infant, with no playmates available during its first month, apparently did not begin social play until the eighth week. This was partly due, however, to 11's unusual persistence in keeping other monkeys from her infant. In general, the mothers' temperament seemed most often to limit the infants' socialization. Almost every infant was at first forcibly restrained by its mother from approaching, or being approached by, other monkeys.

Because of the limitations of field observations, I could identify only the more obvious of the infants' vocal signals (Table 2). Three indicated generalized distress of varying intensity, whereas "mewing" was apparently a more specific signal which functioned as a "lost" call.

TABLE 2. VOCAL SIGNALS OF INFANTS

Signal	Week when first heard	Apparent causes	Mothers' responses
Squeak	1	1. Inf. fell from mother's back 2. Inf. unable to climb onto mother	1, 2. Picked up and held inf.
Gecker	1	1. Inf. unable to locate nipple 2. Inf. treated roughly by mother 3. Inf. left behind by mother 4. Inf. treated roughly by another adult female 5. Inf. handled or carried by sibling or other immature	1, 2. None 3. Returned and carried inf. 4, 5. Picked up and held inf.
Scream	1	1. Inf. fell from mother's back 2. Inf. fell from branch and hung by hands 3. Mother chased another monkey that was near inf. 4. Inf. carried by sibling 5. Siblings fighting near inf. 6. Inf. located (carried?) 100 yards from mother	1. Transferred inf. below 2-6. Ran to inf. and held it
Mewing	7	1. Inf. carried by sibling 30 minutes 2. Inf. left behind 30 ft. in tree 3. Inf. left behind 20 ft. on ground	1. Followed but made no attempt to regain inf. 2, 3. Returned to inf. and carried it

With Their Mothers

For the first day or two after birth an infant typically remained in constant close contact with its mother's body, clutching the skin and fur on her chest and abdomen as she sat or stood, often with one arm around the infant. Occasionally she groomed it for short periods (Fig. 4), but more often she groomed with other members of the band. Females 11 and DR both groomed other monkeys much less than they were groomed. Soon the infants began to spend short periods on the ground out of physical contact with their mothers. Female 11's infant was first seen out of contact on day 2, when she sat aside and watched it lie and crawl on the ground for three minutes. She did this frequently from then on, and as early as day 7 left her infant on the ground as she chased another monkey several yards. DR's infant, less active and with a more restrictive mother, was not seen out of contact until day 12, though it tried to leave and was restrained at least as early as day 6. Neither of the infants was seen out of contact with its mother for more than five minutes at any one time during the first month. Table 3 summarizes all of this activity for females 11 and DR and their infants.

Gradually the infants spent more time out of contact and went farther from their mothers (Table 4). As the females allowed their infants to wander more, they also became less protective and permitted the infants greater social freedom. Finally there came a time when the females essentially no longer restricted their infants' movements or social interactions. This stage of relative independence was reached by some infants as early as the fifth week, though most did not attain it until the seventh or eighth week, and one not until the eleventh week.

The mothers' permissiveness in allowing their infants to leave them in nonsocial situations was apparently not correlated with rank. All six of the primiparous females, however, were among the most restrictive mothers in this respect.

All of the mothers were protective toward their young, usually snatching them up when a fight broke out nearby, or when an alarm call was heard. The mothers also frequently picked up and held their infants when the latter were approached by another monkey. During rain showers each mother sat hunched forward with her infant huddled close in under her chest and abdomen.

Females AS and KA, both primiparous, handled their infants roughly at times. The rougher was KA, who frequently pulled her baby away as it nursed, held it upside down, thumped it on the ground or dragged it around by its arm.

TABLE 3. COMPARISON OF OLD FEMALE 11 AND PRIMIPAROUS FEMALE DR IN PERCENT. OF TIME SPENT WITH THEIR INFANTS AND OTHER MONKEYS DURING THE FIRST MONTH AFTER BIRTH

Female 11 and her infant were observed for 36.4 hours, DR and her infant for 21 hours.

	11 % of time	DR % of time
MOTHER IN CONTACT WITH INFANT		
Mother held infant	58.6	90.4
Mother groomed infant	4.8	0.6
Mother groomed with others		
Her other young	24.6	—
Adult females	5.3	7.3
Immatures	0.7	1.0
Adult males	2.5	0.0
MOTHER NOT IN CONTACT WITH INFANT		
	3.5	0.7
	100.0%	100.0%

During the first month a mother would occasionally turn her infant upside down and touch her lips and/or nose to its perineum (Fig. 5). Though this behavior might aid in olfactory recognition of the infants, it was done usually after the females had been sitting for some time holding their infants, rather than as a greeting. This behavior was not correlated with the age or breeding history of the mothers, or the sex of the infants. Hall & DeVore (1965) reported similar behavior toward infant baboons, but by other males and females which approached the infants and their mothers. These authors interpreted this behavior as a greeting, and Hall (1962) also described perineal mouthing as a form of greeting between adult baboons.

None of the four females whose young were delivered by cesarean section accepted them afterwards in the highly disturbed laboratory situation. After they were returned to the band without their infants, however, three of these females were seen to hold and cuddle other infants.

With Immature Siblings

The schedule of the infants' interactions with

TABLE 4. DISTANCES INFANTS WALKED FROM THEIR MOTHERS AT DIFFERENT AGES

Distance in feet	Day when first seen (range)	Weeks in which most infants attained each distance
1	4-16	1-2
3	6-21	2-3
5	12-34	3-4
10	12-53	4-6
30	34-66	7-9

monkeys other than their mothers is summarized in Table 5.

Some siblings, especially females, were very solicitous. Whenever the infant left its mother they quickly approached and sat by it, and often touched, held, or even carried it. Siblings occasionally picked up infants that were left behind and carried them to their mothers. When another monkey approached the infant a sibling might chase the intruder or hold the infant, and siblings sometimes rushed to take infants that were held by alien adult females. In addition, some siblings, mostly females, played frequently with the infants, whereas others seldom played with or protected them.

With Other Immatures

Immatures of other mothers, especially females, also showed great interest in infants. These immatures usually approached mother and infant, groomed the mother, and while doing so briefly touched the infant. On four occasions I saw an immature female groom an infant for

a few seconds. These immatures rarely had an opportunity to hold or carry infants because of the close watch kept by the infants' mothers and siblings.

Apparently immatures learn to respect the protection infants receive from their immediate families. Infants less than seven weeks old approached immatures 19 times, and on 14 occasions the immatures retreated. Five times the infant was ignored. The rank of the infant's mother had no apparent effect on the reactions of the immatures.

With Other Infants

At first the infants ignored other infants even when they were in physical contact, as when their mothers groomed each other. Within a week the young began to approach and reach for other infants, and in the third week they began to play with them. At first the play consisted of climbing and crawling near each other, with little or no contact. Then they began to touch each other, jump and grab at each other, pull hair,

TABLE 5. SOCIAL CONTACTS OF INFANTS WITH MONKEYS OTHER THAN THEIR MOTHERS

Type of contact	Day when first seen	Weeks when typically seen for first time
With siblings		
Touched by	1	
Groomed by	2	1
Held or carried by	7	Rarely seen
Reached for, approached, touched	5	Rarely seen
Played with	27	2
With other immatures		5
Touched by	4	
Groomed by	8	1
Held or carried by	3	Rarely seen
Reached for, approached, touched	6	Rarely seen
Played with	34	2
With other infants		7
Touched by	4	1
Reached for, approached, touched	4	1
Played with (little or no contact)	15	3-4
Played with (frequent contact)	19	6-7
With mature females		
Touched by	3	1
Groomed by	9	3
Held by	22	Rarely seen
Carried by	18	Rarely seen
Reached for, approached, touched	4	2
With mature males		
Approached	23	8
Touched, climbed on	39	8
Touched by	56	8

wrestle, chase and give inhibited bites (Fig. 6). Contact play was usually fully developed in the sixth or seventh week.

A careful record of each infant's playmates failed to show a general tendency for close relatives to play together a disproportionate amount of the time. The only exceptions were the infants of the two highest-ranking females in the band, which are thought to be mother and daughter or sisters. Though play between close relatives might be more important later, during the first three months the choice of playmates was apparently influenced more by which of the available infants were most active. Some infants were conspicuously more active in play than others, and the most active players were born at various times throughout the birth season. All infants played with other infants much more than they played with their siblings.

With Mature Females

Other females, some of them with infants of their own, frequently approached mothers with infants and either sat a few feet away (Fig. 1) or groomed the mother. Usually the infant was only watched, but occasionally a female would touch or even groom it briefly. Newly mature females, especially, showed an active interest in the infants, and the most persistent of these females was a four-year-old that did not give birth.

Even though mature females usually approached and picked up lone infants not their own, these females sometimes backed off when approached by an infant, just as did the immatures. In 33 observed incidents the female accepted the advance of an infant 18 times, retreated 7 times, hit or pushed it away 5 times, and ignored it 3 times. All of the retreats were from infants whose mothers ranked in the top four, and all five of the hostile reactions occurred when the infants were in their second month. In addition, two females were seen lip-smacking at infants near their mothers, and another female presented her perineum to an infant as it approached, then touched it. Both lip-smacking and presenting are appeasing or submissive acts.

After the seventh week, when the infants became relatively independent of their mothers, other females sometimes followed, held and groomed the infants, and less often carried them. If a female's own infant was present, she held both together. In all observations, the "adopted" infant refused to cling and broke away, or was snatched from the female by one of its siblings. Several times I saw a female pick up another infant when her own was nearby, then pull it from her quickly and forcefully when it did not cling, or when her own infant returned. Twice mature females (seven and nine years old) showed ap-

parent concern and tried to retrieve infants from trees where they were climbing, even though the infants' own mothers ignored them.

With Mature Males

Mature males were never seen to approach infants. As early as the third day, however, mothers with infants groomed males. Though sometimes in contact with the males on such occasions, the infants were always ignored.

After several weeks infants occasionally approached males on their own, touched them and even climbed on them. Each male's responses to such approaches varied from time to time, but some males were more receptive than others to infants. The rank of the males apparently did not affect their responses. In the 25 incidents observed, mature males 7 times ignored infants that approached them, 6 times held them gently in their arms, 3 times retreated from them and 9 times threatened, hit or grabbed at them.

The infants seemed to learn slowly the meaning of aggressive signals. Males threatened infants with direct, open-mouthed stares and head bobbing, and occasionally a male hit an infant or grabbed it and briefly pinned it to the ground. The infants completely ignored this hostile behavior except on one occasion. When a 58-day-old infant approached the highest ranking male, he hit it, and when that had no effect he hit it harder. The infant crouched and gave a slight grin, both typical submissive acts used by adults.

SOCIAL RELATIONS OF MOTHERS

With Their Own Immatures

Mothers were very tolerant toward their young of the previous three years. Some infants from the previous year still nursed occasionally until the new infants were born, but otherwise the immatures' relations with their mothers were little changed. Some immatures, because of their interest in the infant, probably spent even more time with their mothers after the new young arrived than they had before. From the first day, mothers groomed their one- to three-year-olds and let them huddle against the infants (Fig. 7). The immatures were also allowed to touch and even groom the infants. When an infant began to crawl, its mother sometimes restrained it from approaching its siblings and also occasionally hit the immatures when they touched the infant. Several times a one- or two-year-old, sitting beside its mother and infant sibling, suddenly backed or jumped away grinning and screeching for no apparent reason, or when the mother simply shifted her position.

It is enlightening to compare the mothers' relative protectiveness from month to month and

TABLE 6. RELATIVE PROTECTIVENESS OF MOTHERS TOWARD INFANTS AT DIFFERENT AGES AND IN THE PRESENCE OF DIFFERENT ASSOCIATES

The indices show the percent of potential physical contacts between infants and other monkeys which were prevented by the infants' mothers. N = the number of incidents observed.

Infants' associates	1st month		2nd month		3rd month	
	N	Index (%)	N	Index (%)	N	Index (%)
Other infants	41	22.0	284	3.9	229	1.7
Immature siblings	95	27.4	42	11.9	4	0.0
Other immatures	75	70.7	35	34.3	27	7.4

in respect to different categories of associates. This trait can be shown by the per cent. of potential physical contacts (between infants and the members of a given category) which were prevented by the mothers (Table 6). The mothers prevented such contacts by restraining their infants from approaching, or by chasing off, the other monkeys. For example, during the first month the mothers prevented 27.4% of the potential physical contacts between infants and their siblings, and allowed 72.6% of the attempted contacts to occur.

During the second month mothers rarely hit their immatures when they approached the infants, though female 11 continued to do so occasionally as late as day 53. Siblings were occasionally allowed to carry infants in the second month, and female 11 was especially tolerant in this respect. On day 46, her three-year-old daughter carried the infant several hundred yards during a half hour period. Female 11 stayed within 20 feet of the pair and twice sat touching them, but made no attempt to regain the infant. Three times 11 chased three- or four-year-old females that approached her two young. All of the other instances of siblings carrying infants were for short distances, usually when the mother walked away and left her infant behind.

In the third month the infants associated chiefly with their peers, and only four meetings, all unrestricted, were seen between infants and their immature siblings.

Besides the aforementioned indices, protec-

tiveness is also indicated by the ages at which infants achieve relative social independence from their mothers. By neither criterion did primiparous mothers differ appreciably from multiparous ones. There were also no marked differences between high- and low-ranking females in the age at which their infants achieved independence, and the protective indices revealed no consistent differences in the protectiveness of mothers of different rank in the presence of their own immatures or other infants. There was, however, an apparent tendency for higher ranking females to be more protective in the presence of other immatures (Table 7). These figures are suggestive, but too much importance should not be attached to them because of the small sizes of most of the samples. It is to be expected that manifestations of rank would be weak or absent in most of the behavior observed during this study. It is known that a mother's rank tends to be passed on to her offspring, but this is probably accomplished through her intervention during disputes over such items as food and resting places, and by the passive respect shown her and her young by lower-ranking adults. During the first three months the infants are nursing, their behavior is chiefly exploratory and nonagonistic, and other monkeys either ignore them or are friendly. There is some evidence that the young do not respect rank themselves until they are several years old. For example, the immatures' behavior toward the infants was evidently not affected by the mothers' rank, but the behavior of adult females was.

TABLE 7. RELATIVE PROTECTIVENESS OF MOTHERS OF DIFFERENT RANK IN THE PRESENCE OF THE IMMATURES OF OTHER FEMALES

The indices show the percent of potential physical contacts between infants and these monkeys which were prevented by the infants' mothers. N = the number of incidents observed.

Rank of mother	1st month		2nd month		3rd month	
	N	Index (%)	N	Index (%)	N	Index (%)
High	48	85.4	14	57.1	12	16.7
Low	21	52.4	16	25.0	7	0.0
Medium	6	16.7	5	0.0	8	0.0

With Other Immatures

Immatures other than siblings were allowed to touch and groom infants as early as the third day. These immatures also groomed the mothers and were groomed by them as early as the fourth day. However, the mothers were much more protective in the presence of other immatures than in the presence of their own immatures. Some mothers were not seen to chase other immatures from their infants after the third week, but others did so into the third month. Old female 11, though more permissive in allowing her infant out of contact, was much more protective than primiparous DR in the presence of other monkeys during the first month. Thus, 11 chased immatures seven times as often as she permitted contact, while DR permitted contact as often as she prevented it. The former continued to restrict contacts as late as day 51, while DR was not seen doing so after day 27.

During the second month immatures were allowed to touch and groom the infants more than before. They began playing with some of the infants as early as the fifth week, but with most of them not until the sixth to ninth week. Although one primiparous female chased immatures from her infant as late as day 66, all mothers allowed their infants to play with immatures in the third month.

With Other Infants

During the first month mothers usually let other infants approach, touch and even play with their own infants. The first contacts were permitted during the first week, and play was permitted commonly as early as the third to fourth week. Most mothers stopped restricting infant-infant contacts entirely during the fifth to seventh week, but a few still restricted contacts between infants as late as the twelfth week.

As mentioned above, some mothers showed interest in other females' infants. During 21 hours of observation in the first month after her infant was born, DR approached the infants of other females 14 times, whereas in 36 hours of observation, 11 approached none.

With Mature Females

The effect of parturition on relations between mature females is complicated by the year-round tendency for these females to sit near and groom each other. There is certainly an increase in these activities when young are born, but we have no quantitative measure of it. Mothers let other females sit within a few feet of them the day the young were born, and also exchanged grooming with these females beginning in the first week. Other females likewise handled and groomed the infants during the first week. DR permitted such

handling by another female as early as the fifth day, while 11 was not seen to do so until day 16. During the first month mothers chased other females, or restrained infants from them, 1/4 as often as they permitted such females to sit near them, groom with the mother, or handle the infant. Because these figures include sitting near and grooming the mother, they are not strictly comparable to the protective indices for immatures and other infants. During the second month mothers chased other females or restrained infants from them only 1/7 as often as they tolerated such females. Some mothers were not seen to interfere with infant-female contacts after the third week, while others did so until at least the end of the seventh week. During the third month mature females were seen holding or grooming infants not their own on eight occasions, and no restriction of such contacts was observed.

The females' rank had no effect on which ones were permitted to sit near a mother and infant. In 80% of the grooming sessions between mothers and other mature females, however, the lower ranking female was the groomer. This percentage does not include the frequent grooming between mothers and daughters. Of the other females allowed to hold or carry infants (excluding close relatives), three-fourths were of lower rank than the mothers. Mothers of new infants were apparently groomed more in the first month after birth than in the succeeding months.

With Mature Males

On the day of birth, females carrying newborn young fed in the usual manner among crowds of mature males and females. Females with infants groomed adult males as early as the third day, and the mothers tolerated contact between the males and infants at such times as long as the males ignored the infants. The first potential infant-male contact away from the mother was observed on day 23, when an infant approached male 56. As 56 started to leave, the mother rushed over, grinning, grabbed her infant and ran away. The next such incident was observed on day 39, when 11's infant approached and touched male 14. He ignored the infant and 11 did not interfere. All of the other contacts observed occurred during the seventh week or later when infants approached males. The infants were relatively independent by this time and only once did a mother interfere. This incident involved female 11's infant on the 58th day, and suggests how the offspring of a high-ranking female may achieve high rank under its mother's protection, as suggested by Koford (1963). As 11 sat watching three feet away, the infant approached male 08 and climbed all over him. At first he ignored it, but after a few seconds 08

jumped up, ran a few steps, stared, and bobbed his head at the infant. As it approached again, 08 continued to stare and bob his head and when the infant reached him he hit it. Immediately 11 attacked 08 and chased him 20 feet. The infant quickly approached 08 again and touched him. 08 jumped back at the touch, then ran off as 11 ran toward him. Eight days later as he was groomed by 11, 08 held 11's infant in his arms and let it climb on him.

COMPARISON WITH OTHER STUDIES

Because the emphasis in this study was on the social relations of infants and their mothers, little of the information collected in laboratory studies is directly comparable. With a few exceptions, the individual behavior of the laboratory monkeys, especially those studied by Hines (1942) and by Tinklepaugh & Hartman (1932), developed at approximately the same rate as the behavior of those which I observed in the field. Sitting up, hopping, climbing, handling objects and playing all developed at about the same age in the laboratory and in the field. The two infants studied by Foley (1934) and by Lashley & Watson (1913) did not begin standing or walking until the 11th and 13th day, respectively, while the other laboratory infants and the infants in the field all did so during the first week. Unsupported bipedal standing, observed during the fourth week in the field, was reported in the laboratory only by Hines, who first recorded it in the sixth week. The infants studied by Hines began vertical jumping in the fourth week, about the same time as did those in the field. But jumping was not observed by Lashley & Watson until the seventh week, and not by Foley until the fourteenth week. It was evident in the laboratory studies, just as it was in the field, that the close relationship between mothers and their infants delayed the performance of some actions of which the infants were physically capable. For example, the infants observed by Tinklepaugh & Hartman were able to walk as early as the first day in their solitary testing periods, but did not walk away from their mothers until the eighth to tenth day.

The individual behavior reported by Hinde, Rowell, & Spencer-Booth (1964) for infants in social groups in outdoor runs was very similar to that seen on Cayo Santiago. Such activities as walking, climbing, and mouthing and handling foreign objects all developed at about the same ages in both studies. There were two conspicuous differences, however. Bipedal locomotion for a distance of several feet occurred only occasionally in Hinde's colony, from the seventh week on. On Cayo Santiago this behavior appeared in the second week. Furthermore, none of Hinde's

monkeys rode on their mothers' backs until the 17th day, and most of them began in the third or fourth week. Hinde, Rowell & Spencer-Booth observed that the mothers frequently tried to pull the infants to a ventral position, and they concluded that rhesus mothers do not like carrying their babies on their backs. On Cayo Santiago this behavior appeared as early as the fourth day, was very common with some individuals, and was frequently encouraged by the mothers. Though this particular study covered only the first three months after birth, other observations show that dorsal riding is common among older immatures in the Cayo Santiago colony.

A few comparisons can be made of the socialization of infants in the laboratory and on Cayo Santiago. Hansen's (1962) study of mother-infant interactions revealed decreasing ventral contacts, cuddling, nursing and grooming during the first three months. He called this period the stage of "maternal attachment and protection." The mothers' tendency to restrain and retrieve their infants declined sharply and then leveled off at about 60 days. Rosenblum (1961) recorded an initial increase in social play among infants, with a plateau reached at the end of the second month. Thus the age at which the infants reached a stage of relative independence from their mothers (second to third month) was roughly the same in these restricted experimental set-ups as in the field.

Hansen's mothers could interact only with their own and other infants, and he recorded much positive and negative behavior toward the other infants by the mothers. This sort of behavior was much less common on Cayo Santiago, where the mothers interacted more with older monkeys. Hansen concluded from his study that active rejection by the mother was more important than previous field studies had indicated in contributing to the infants' independence. He pointed out, however, that this rejection may have been accentuated by the laboratory situation, and I am inclined to agree with this. On Cayo Santiago rejection of infants seemed insignificant compared to the infants' interest in other monkeys, especially other infants. From preliminary studies, Harlow, Harlow & Hansen (1963) reported no significant differences in the maternal responses of primiparous and multiparous mothers. This tentative conclusion agrees with my observations on Cayo Santiago.

The social behavior of the infants observed by Hinde, Rowell & Spencer-Booth was also similar to that of the Cayo Santiago infants. The qualitative descriptions by Hinde, Rowell & Spencer-Booth of the positions of infants on mothers, of nursing, of carrying, and of play apply equally to

the Cayo Santiago monkeys. Even the frequency of mother-infant grooming (less than 5% of total time) was similar in the two studies. The infants in their colony first broke contact with their mothers and first walked away from them at about the same ages (1-2 weeks) as the infants on Cayo Santiago. As in the Cayo Santiago colony, the apparent development of locomotor patterns by the infants was affected by the restrictions imposed by their mothers and by the attractiveness of other monkeys. Social play began at about the same age in both colonies, but in Hinde's colony it was restricted by the mothers for the first 8-10 weeks, whereas on Cayo Santiago such restriction stopped about two weeks earlier. Grooming of infants by other adult females was common in both colonies, but in neither colony did adult males groom infants during the first three months. Hinde, Rowell & Spencer-Booth saw tentative grooming of mothers by infants very rarely, and I never observed it.

The three generalized distress calls which I heard infants use were used in similar contexts by Hinde's infants, but apparently the mewing "lost call" was not given in his colony—probably because the runs were too small for the infants to get "lost." The "fear grin" was apparently not used by infants less than ten weeks old in Hinde's colony, whereas a slight but clearly recognizable grin was given in the appropriate context by a 58-day-old infant on Cayo Santiago.

Rowell, Hinde & Spencer-Booth (1964) also reported on the relations between infants and "aunts"—other females in the same band. As on Cayo Santiago, these females tended to sit near the mother and groom her to get near the infant. However, grooming of the infants by "aunts" did not begin in their colony until the fourth week, while on Cayo Santiago it began in the first week. Other females carried and cuddled infants in the first three months in both studies, and in Hinde's colony "aunts" began playing with the infants in the sixth week. Adult females were not seen playing with infants on Cayo Santiago, but Rowell, Hinde & Spencer-Booth included among the "aunts" females two and three years old. I included these young females among the "immatures," which began playing with the infants at about the same age. Relative social independence from their mothers was achieved in the second or third month by infants in both colonies. Finally, Rowell, Hinde & Spencer-Booth reported no consistent differences in the behavior of "aunts" which ranked higher and lower than the mothers, although the mothers permitted contact between infants and subordinate "aunts" more often than between infants and "aunts" who outranked the mothers. This agrees with my observations on Cayo Santiago.

The only information available on the early development of rhesus infants in their native India is that provided by Southwick, Beg & Siddiqi (1965) on the behavior of one infant and its mother during the first week after birth. Their account generally agrees with the data from Cayo Santiago.

To sum up, the individual and social development of rhesus infants in captivity and in the field is very similar for those patterns which are appropriate to the captive situation. Certain social patterns are especially apt to be lacking in the laboratory where social interaction is severely limited. Not surprisingly, the few differences in rate of development that are apparent in the two situations indicate a slightly retarded development (or use) in captivity, especially of social acts. Such differences are probably due to a combination of individual differences (accentuated by the small size of most laboratory samples), and the social restrictions of the captive colonies. The Cayo Santiago colony is itself a "captive" one, but the social environment for very young infants is probably essentially like that in wild bands in India. A more detailed study of infant development on Cayo Santiago would be both feasible and highly desirable.

SUMMARY

The behavior of infant rhesus monkeys and their mothers during the first three months after birth was studied in the free-ranging colony on Cayo Santiago. Newborn infants clung to their mothers' venters, but began to sit and crawl on the ground as early as the second day. Some traveled ten feet in the third week. Climbing on vines and bushes became common in the second to third week. At first an infant would cling below as its mother walked, but as early as the first week a few began riding on her back part of the time.

The infants' movements and social interactions were restricted by their mothers for about seven weeks. Siblings were frequently allowed in contact with the infants from the first day, but contacts with other immatures were severely limited during the first month. Toward other infants the mothers were much more tolerant. Play with immatures and other infants was common by the seventh week. Other mature females tended to gather around and groom mothers with infants. These females were generally allowed to touch the infants during the first week. Although adult males usually ignored the infants, they were sometimes hostile when the infants approached.

Some mothers who were relatively permissive in allowing their infant to leave them in nonsocial situations were relatively protective in the

presence of other monkeys. Primiparous mothers tended to be restrictive in the former respect, but permissiveness was not correlated with social rank. Protectiveness in social situations was not correlated with past breeding history, and not obviously with rank. High-ranking mothers, however, tended to be more protective in the presence of the immature offspring of other females.

Comparison of the Cayo Santiago infants with those in laboratories and outdoor runs shows close agreement in the rates of development of most kinds of behavior. The exceptions were chiefly in social behavior, and were probably due to a combination of individual differences and the more complex social environment on Cayo Santiago.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Two pregnant females watch as the band's highest-ranking female nurses her month-old infant.
- FIG. 2. Female DR's 2-mo.-old infant clings below as she walks. A 4-yr.-old female submissively presents her perineum.

PLATE II

- FIG. 3. A 3-mo.-old infant rides on its mother's back as she feeds near the band's highest-

ranking male.

- FIG. 4. A mother grooms her 2-wk.-old infant.

PLATE III

- FIG. 5. A mother holds her infant upside down as she mouths its perineum.

PLATE IV

- FIG. 6. A mother sits unconcernedly as her 7-wk.-old young plays with another infant.
- FIG. 7. A yearling sits in contact with its mother and infant sibling.